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## Palaeontology

## Evidence for a giant parrot from the Early Miocene of New Zealand

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Insular avifaunas have repeatedly spawned evolutionary novelties in the form of unusually large, often flightless species. We report fossils from the Early Miocene St Bathans Fauna of New Zealand that attests to the former existence of a giant psittaciform, which is described as a new genus and species. The fossils are two incomplete tibiotarsi from a bird with an estimated mass of 7 kg, double that of the heaviest known parrot, the Kakapo *Strigops habroptila*. These psittaciform fossils show that parrots join the growing group of avian taxa prone to giantism in insular species, currently restricted to palaeognaths, anatids, sylvornithids, columbids, aptornithids, ciconiids, tytonids, falconids and accipitrids.

## 1. Background

Insular avifaunas are renowned for the evolution of novelties, usually in the form of extraordinarily large and flightless members of widespread and well-known lineages [1–4]. Preeminent among these is the columbid Dodo *Raphus cucullatus* of Mauritius [5], but the list includes giant Sylviornithidae on New Caledonia (*Sylviornis*) and Fiji (*Megavitiornis*) [6–8], other giant columbids on Rodrigues (*Pezophaps*) and on Fiji (*Natunaornis*) [5,9], giant waterfowl on Hawaii [10] and Malta [11], a giant ciconiid stork on Flores, Indonesia [12], and giant tytonid owls and other raptors in the Caribbean [13–16]. Insular rails (Rallidae) tend to be larger than mainland relatives, but the largest, the Takahe (*Porphyrio hochstetteri*) from New Zealand (NZ), at up to 3.2 kg, is smaller than these insular giants [17,18]. We treat all of these as examples of autapomorphic giantism, *sensu* Gould & MacFadden [19] rather than extremes of the Island Rule phenomenon, where size is relative to close mainland relatives [20,21].

Since moa were first reported in 1839 [22], NZ has become recognized as the epitome of the phenomenon of island giantism in birds. In addition to nine moa species (Dinornithiformes), two flightless anserines (*Cnemiornis*, Anatidae), two gruiforms (*Aptornis*, Aptornithidae) and a huge eagle (*Hieraaetus moorei*, Accipitridae) evolved from small ancestors into giant elements of the Holocene avifauna [23–28]. The assembly of this unique NZ Holocene fauna has recently been informed by the Early Miocene (19–16 Ma [29–31]) St Bathans Fauna from Otago, the only window into NZ pre-Quaternary terrestrial avifaunas [32,33]. Moa, *Aptornis*, an indeterminate eagle and precursors of *Cnemiornis* have been reported from the fauna [33]. Despite two decades of exploration and the recovery of thousands of fossils, the specimens described here are the only ones representing this new taxon. They reveal yet another striking example of island giantism in birds.

## 2. Methods

The fossils, catalogued in the Museum of New Zealand Te Papa Tongarewa collections, are shafts of left and right tibiotarsi probably of one individual (see electronic supplementary material, data). They were compared to a wide range of bird skeletons in the South Australian Museum collection and to images on the Smithsonian National Museum of Natural History website for the bird collection (<https://collections.nmnh.si.edu/search/birds/>) see Field/Special collections/Synoptic skeleton images.

## 3. Description

The left tibiotarsus is most complete. Lacking both ends, it preserves the shaft from the base of the cnemial crests, including the complete fibular crest, to just distal to the pons supratendineus. Caudal to the distal end of the crista cnemialis cranialis on the shaft margin, the medial facies is flattened and lacks an impressio ligamentum collateralis medialis. The lateral margin of the fibular crest is straight and arises smoothly from the shaft proximally and, distally, becomes increasingly prominent. The cranial and caudal facies of the shaft adjacent to the fibular crest are convex and lack cristae. Distal to the fibular crest, a linea intermuscularis cranialis extends distally and cranially in an even curve to be near centred on the shaft by midlength; it then extends distally to the lateral side of the laterodistal insertion of the transverse ligament (retinaculum extensorium tibiotarsi). Distally, the shaft widens asymmetrically, mainly medially. Most distinctively, robust raised and ovoid scars approximately 10 mm long mark the insertions of the transverse ligament. Both are proximal to the pons supratendineus: the distolateral scar separated by 3 mm, the proximomedial one by approximately 11 mm. Scars for the fibular retinaculum are prominent: that mediocranially, fused with the transverse ligament distolateral scar; that laterally, more elongate, overlapping proximally the distal insertion of the transverse ligament and distally the pons. The sulcus extensorius is slightly offset medially from the shaft centre, relatively shallow and lacks bounding cristae. The pons is preserved as two co-level projections separated by 4 mm. Their proximodistal length (3 mm) is much shorter than the sulcus extensorius width (5 mm). While the projections are somewhat worn, the presence of cristae rising to the tip of the medial one on its proximal and distal margins, show that the pons was not fully ossified and that in life these two projections were connected by ligament. Distal to the pons, no facet for the articulation of the eminentia intercotylaris of the tarsometatarsus is apparent. The shaft at the level of the pons is much flattened, 1.7 times wider than deep.

## 4. Comparisons

Despite lacking the proximal and distal ends, the specimens display an autapomorphic character suite developed from Worthy *et al.* [34] that defines them as a psittaciform as follows: (1), the sulcus extensorius is located near mid-shaft; (2), shaft **widens symmetrically** distally and is distinctly craniocaudally flattened; (3), pons supratendineus present and (4) aligned horizontally, and (5) reduced; (6), large and prominent insertion scars for the transverse ligament with the distolateral scar distinctly proximal to the pons. In combination, this suite of characters distinguishes parrots from

all other birds as shown by the following comparisons: Palaeognathae differ in (1), having the sulcus extensorius located medially, in line with the medial condyle and (2), having distal **width expanded** medially and shaft cranio-caudally deep. Neognathae: (1) distinguishes all gruiforms, cariamiforms, phoenicopteriforms, ciconiiforms, procellariiforms, otidids, ardeids and threskiornithids (sulcus located distinctly medially); (2) also distinguishes all these taxa (distal end deep **with asymmetric** medial expansion); (3) distinguishes hornbills (Bucerotidae) and all strigiforms (lack a pons) and falconiforms (characterized by an ossified pons with three openings); (4) distinguishes galliforms, cariamiforms, peleciforms, accipitriforms (pons angled, medial side offset proximally relative to the lateral side); (5) pons reduction, such that it is short, with incomplete ossification is limited to few taxa, e.g. apterygids (Palaeognathae) distinguished above, and a few larger psittaciforms (e.g. *Lophopsittacus*, *Necropsittacus*, *Tanygnathus*, *Psittichas*, *Psittacula*, most cakatuids, several Arini, and the NZ *Strigops habroptila* [34,35]. In *S. habroptila*, the pons may be a complete ossified bridge, albeit proximodistally narrow, or incomplete; (6) configuration of the transverse ligament distinguishes anseriforms, galliforms, phoenicopteriforms, charadriiforms, accipitriforms, ciconiiforms, cariamiforms, gruiforms, eurypygiforms, procellariiforms, peleciforms, otidids, threskiornithids, ardeids, cuculiforms and passeriforms (all species of which have the distolateral insertion laterally alongside the pons). Some columbiforms (e.g. notably the raphine clade of *Raphus*, *Natunaornis* and *Goura*) are also distinguished by having the distolateral insertion laterally adjacent to the pons [9,36]. However, the ptilinopine columbids (e.g. *Ducula*), are similar to psittaciforms with the distolateral insertion of the transverse ligament proximal to the pons, but differ with a marked crista bounding the sulcus extensorius laterally. In no columbiform is the pons incomplete.

The St Bathans tibiotarsi are much stouter than the short peleciform ones or the very elongate ones characterizing otidids and the waterbirds ciconiiforms, phoenicopteriforms, ardeids and threskiornithids. These latter waterbirds further differ in having a prominent facet for the reception of the eminentia intercotylaris.

The large and robust nature of the fossil (least-shaft circumference 35.8 mm) leads to an inferred body mass of 6.96 kg using Campbell and Marcus's [37] algorithm for tibiotarsi of all taxa. This suggests that it was from a terrestrial bird and precludes it from likely affinity with small arboreal or aerial taxa, of which passerines are distinguished by (6) above. As the fossil shares the autapomorphic character suite distinguishing psittaciforms from all other neornithines, we conclude that these St Bathans fossils represent a psittaciform. However, it was more than twice the mass of the largest known parrot, Kakapo *Strigops habroptila* (Strigopidae) (3.0 kg) [38]. We therefore name it, but do not assign it to a family because its relationships to NZ Nestoridae and Strigopidae, or more derived families, cannot be established at this point.

## 5. Systematic palaeontology

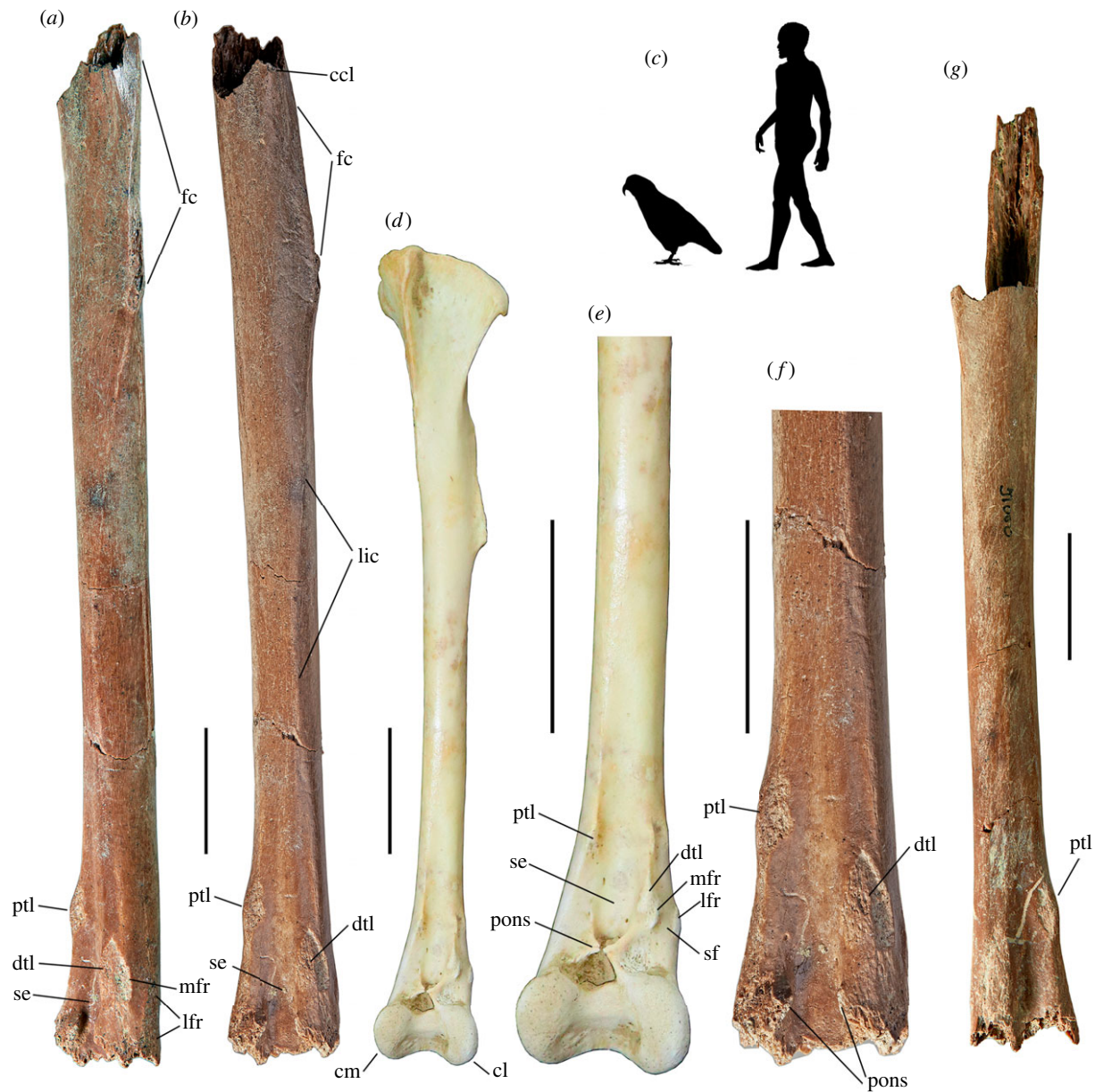
Aves Linnaeus, 1758

Psittaciformes Wagler, 1830

?Strigopoidea Bonaparte, 1849







**Figure 1.** Tibiotarsi of *Heracles inexpectatus* gen. et sp. nov., left, holotype (*a,b,f*) NMNZ S.51083 and right, paratype (*g*), compared to (*d,e*) left tibiotarsus of *Strigops habroptila* (Canterbury Museum Av45277), in craniolateral (*a*) and cranial (*b–g*) views. (*c*) Silhouettes of a human and *Heracles* for scale. Scale bars are 20 mm. Abbreviations: ccl, crista cnemialis lateralis; cl, condylus lateralis; cm, condylus medialis; dtl, distal insertion scar for transverse ligament; fc, fibular crest; lfr, lateral scar for fibular retinaculum; lic, linea intermuscularis cranialis; mfr, mediocranial scar for fibular retinaculum; pons, pons supratendineus; ptl, proximal insertion scar for transverse ligament; se, sulcus extensorius; sf, sulcus m. fibularis; trf, tuberculum retinaculi m. fibularis. Human silhouette from PhyloPic <http://phylopic.org/image/f33e111a-7257-4ad0-a2c1-663663784d3f/>, by T.M. Keesey. (Online version in colour.)

***Heracles inexpectatus* gen. et sp. nov.**

<http://zoobank.org:act:538A92AA-8288-4B28-8979-2742D9EA1E6E>

<http://zoobank.org:pub:A5200684-97E6-4370-A4A3-2DE640CD8019>

**Holotype:** NMNZ S.51083 (figure 1), a partial left tibiotarsus preserved from the proximal side of the fibular crest to just distal to the pons supratendineus.

**Paratype:** NMNZ S.51080, a matching partial right tibiotarsus preserved from the distal end of the fibular crest to the distal side of the pons, collection data as for the holotype.

**Diagnosis:** A psittaciform much larger than *Strigops habroptila*, with the pons supratendineus incompletely ossified, insertion scars for the transverse ligament very large, both located proximal to the pons, the proximomedial one projecting medially, and the tuberculum retinaculi m. fibularis medialis robust, and relatively close to the condylus lateralis.

**Type Locality:** Bed HH1b, Trench Excavation, foot of hill 50 m east from river bank, at 44.90780° S; 169.85844° E; Manuherikia River, Home Hills Station, Otago, NZ; collected 14 January 2008.

**Stratigraphy and age:** A conglomerate, 9.5–9.58 m above base of Bannockburn Formation, Early Miocene, 19–16 Ma [32], electronic supplementary material, data.

**Etymology:** The nestorid *Nelepsittacus* from the St Bathans Fauna was named after Neleus. This much larger psittaciform is named after the Greek Heracles, who in Latin was known as Hercules, and who killed Neleus and his sons, except for Nestor. Genus gender masculine. The specific epithet denotes the unexpected nature of this find.

**Measurements (mm):** Holotype (paratype): preserved length 161(147), length fibular crest 42, width at distal side of fibular crest 14(13.2), depth at distal end of fibular crest 10(10), length from distal end of fibular crest to middle of

pons 109, minimum shaft width 10.8(10.8), width at middle of pons 17, craniocaudal depth at middle of pons 9.8.

## 6. Discussion

Taphonomic limitations of the littoral depositional environment for the St Bathans Fauna resulted in bones larger than 10 cm long being very rare; only small bones or fragments of large taxa are found [33]. Nevertheless, giant birds represented in this fauna include moa, *Aptornis*, an eagle and large anatids [32,33]. The holotype of *Heracles inexpectatus* is the largest fossil bone known among several thousand specimens in the fauna and adds a giant psittaciform to it.

The St Bathans Fauna has already revealed evidence for an Early Miocene radiation of parrots (Psittaciformes) in NZ, with three small nestorids described in *Nelepsittacus*, and another the size of *Nestor notabilis* [34]. Extant nestorids are grouped in *Nestor* as the sister taxon to *Strigops habroptila*; the two groups combined form the NZ endemic clade (Strigopoidea) that is the sister taxon of remaining psittaciforms [39]. *Strigops habroptila* is the heaviest and only flightless psittaciform [38,40], with legbones the largest among parrots [35]. *Heracles inexpectatus* has similar proportions and morphology to *S. habroptila*, but is much larger, differing qualitatively in greater medial projection of the proximomedial scar of the transverse ligament and less projection of the lateral fibular retinaculum scar (figure 1; electronic supplementary material SI), the last relating to less climbing ability [34]. All known fossil parrots are much smaller than *Strigops* [34]. Given this similarity and its provenance, the affinity of *Heracles inexpectatus* may lie with Strigopoidea. The short separation of the mediocranial fibular retinaculum scar from the condyle suggests closer affinity to strigopids than nestorids [34].

*Heracles inexpectatus* adds to the suite of insular birds that have evolved giant and often flightless forms. This phenomenon is not restricted in taxonomic scope, but instead occurs across a surprising spectrum of groups including palaeognaths, anatids, sylvornithids, columbids, aptornithids, ciconiids, tytonids and accipitrids [5–7,9,10,14,15,24]. Of these, only the restriction of palaeognaths to older and larger continental islands (NZ, Madagascar, New Guinea and associated islands) follows a common pattern. For all truly oceanic islands and the smaller more isolated continental islands (e.g. New Caledonia, Viti Levu) where faunas

derive from dispersal [2], usually only one group spawned giant forms. However, which group did so follows no obvious pattern. For example, there are giant flightless columbids only on the Mascarenes and Viti Levu. It seems likely that the stochastic although often-times directional nature of successful dispersal [41] and competitive exclusion by original founder species [42,43] is what constrained the evolution of giant birds on smaller isolated islands. If the first to arrive on an island was a megapode or a pigeon, then they had free reign to occupy the giant bird niche. Giantism in insular birds appears to have been associated with niche expansion [21], usually into browsing niches occupied by mammals in continental settings. The NZ mainland is larger and more ecologically complex than most islands and, lacking mammalian predators, predictably has produced the greatest diversity of giant avians anywhere [24,33]. Niche expansion is also seen in the surprising example of the mystacinid bats in NZ, that from the Early Miocene, took up terrestrial niches to a greater extent than other bats, became large and adopted a very diverse diet [21,44]. Here, we extend this understanding about the diversity of giant avians by revealing that in the Early Miocene, when NZ had a highly diverse subtropical flora, including casuarinas, palms and diversity of laurels [29–31], an abnormally large species of parrot evolved—*H. inexpectatus*—the first known giant psittaciform.

**Data accessibility.** All data are included herein or in the electronic supplementary material.

**Authors' contributions.** T.H.W. conceived the study. T.H.W., M.A., S.J.H. and R.P.S. conducted fieldwork. T.H.W., R.P.S. and V.L.D.-P. determined and assessed morphological traits. R.P.S. measured and imaged *Strigops* specimens. T.H.W. drafted the manuscript. All authors discussed the results, edited the manuscript, approved the final version and agree to be held accountable for the content.

**Competing interests.** We declare we have no competing interests.

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